PLEISTOCENE BENTHIC FORAMINIFERA FROM IODP SITE U1344:

NORTHERN SLOPE OF THE BERING SEA

A Thesis

by

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ABSTRACT

The Mid-Pleistocene Transition (MPT), one of the largest climate shifts in the late Quaternary, was characterized by widespread, gradual global cooling accompanied by expansion of Northern Hemisphere ice sheets and a shift towards higher amplitude glacial - interglacial cycles. This study utilizes a benthic foraminiferal fossil record recovered from IODP Expedition 323: Site U1344 (3200mbsl, 59° 3.0'N, 179° 12.2'W) on the northern slope of the Bering Sea to understand changes in the deep waters of the Bering Sea that occurred over the last ~1.9Ma. The benthic foraminiferal fossil record at this site is characterized by low oxygen tolerant and deep infaunal groups, which are characteristic of high surface productivity. Although glacial – interglacial changes are not resolved in this record, large shifts in the benthic foraminiferal assemblage – including changes in abundance and diversity – are evident through the MPT. The largest change in the benthic foraminifera assemblage occurs around 0.9Ma and correlates with fluctuations in other proxy records such as diatoms, biogenic opal, and sedimentation from nearby slope Site U1343 (1950mbsl, 55° 33.39'N, 176° 12.2'W) which suggest the expansion of sea ice over both sites. Two species make up the majority of the benthic foraminiferal record at Site U1344: *Elphidium batialis* and *Valvulineria sadonica*; their relative abundances are anti-correlated. Cluster and principal coordinate analyses suggest that these two species represent opposite ends of the environmental gradient at Site U1344. Their records, along with other common

species present at Site U1344, imply that the assemblage variations are primarily dependent upon the type of organic matter reaching the sea floor.

DEDICATION

For my father.

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INTRODUCTION

The Pleistocene Epoch encompasses the onset of northern hemisphere glaciation (NHG) in the earliest Pleistocene (2.4Ma) and a shift in climate periodicity from 41 kyr to higher amplitude 100 kyr glacial-interglacial cycles during the Mid-Pleistocene Transition (MPT, 1.25-0.7Ma) (Elderfield et al., 2012). Altered paleoceanographic conditions due to gradual widespread cooling and the expansion of sea ice had a major impact on benthic marine faunas throughout the Pleistocene (Hayward et al., 2002). Although many paleoceanographic studies have focused on this time period, very few studies have targeted high-latitude regions despite the fact that large-scale, widespread climatic alteration is thought to be amplified in polar regions. This study focuses on a Pleistocene record of abyssal benthic foraminifera obtained from Site U1344 cored during Integrated Ocean Drilling Program Expedition 323, which was the first cruise to sail to the Bering Sea (2009) with the primary intent of recovering sediment cores suitable for the study of high-resolution Pliocene-Pleistocene paleoceanography and paleoclimatology.

Present Day Physical and Oceanographic Setting of the Bering Sea

The Bering Sea is the third largest marginal sea in the world (Takahashi, 2005). It lies between 50-65°N and is connected to the North Pacific Ocean via the Aleutian Passes and to the Arctic Ocean via the Bering Strait (Figure 1). The bathymetry of the Bering Sea includes a shallow shelf (0-200 mbsl) to the northeast and the deep Aleutian

Basin (up to 3500mbsl) to the southwest. The Aleutian Basin contains two bathymetric highs: Shirshov Ridge to the west and Bowers Ridge to the south. The northern continental shelf edge presently determines the extent of perennial winter sea ice (Takahashi, 2005), which begins to form in November and reaches a maximum extent by March (Kim et al., 2011). Strong spring diatom blooms occur annually as the ice melts, and less frequent and shorter blooms occur when sea ice extends past the shelf and nutrients brought by upwelling contact the diatoms living at or near the base of the ice (Alexander and Niebauer, 1981). The open waters of the basin are generally sea ice-free, as warm North Pacific water enters through the passes and travels northwest along the shelf edge (Cassie et al., 2010). Three major rivers drain into the Bering Sea: the Kuskokwim River and the Yukon River, which both originate in Alaska, and the Anadyr River, which flows from eastern Siberia. Deeply incised canyons line the shelf edge and supply terrigenous sediment to the deeper parts of the basin (Aiello and Ravelo, 2012).

Surface circulation in the Bering Sea is predominantly counterclockwise but deviates from its path along the Aleutian Islands and at Shirshov and Bowers Ridges (Cook et al., 2005; Figure 2A). North Pacific water flows into the Bering Sea from the south through the deeper Aleutian passes: Amchitka Strait (1000 m depth), Near Strait (2000 m depth), and Kamchatka Strait (4000 m depth) (Takahashi, 2005; Figure 2B). Warm water from the Alaskan Stream flows in through the Amchitka Strait where it intermingles with the cooler Subarctic Current from the west (through Near Strait) and forms the Bering Slope Current (BSC) which then flows northward along the shelf edge (Cook et al., 2005; Takahashi, 2005). The wax and wane of this warm current can have a

strong impact on water mass geometry, the degree of stratification, phytoplankton blooms, and the supply of nutrients to the Bering Sea slope (Kim et al., 2011).

The Bering Sea experiences high boreal summer insolation and is one of the most productive regions in the world (Aiello and Ravelo, 2012; Kim et al., 2011). Currently, the combination of lateral convection and tidal mixing along the shelf edge due to the BSC brings nutrients up to the surface layer which enhances phytoplankton growth, forming a zone of high biological productivity known as the "Green Belt" (Springer et al., 1996; Cook et al., 2005; Expedition 323 Scientists, 2011). This results in high organic carbon flux to the sea floor and the deposition of many siliceous microfossils including radiolarians, diatoms, and sponge spicules (Aiello and Ravelo, 2012). Today, a well-developed oxygen minimum zone (OMZ) exists in the Bering Sea from ~700 to 1600m water depth (Takahashi, 2015; Figure 3), resulting from high organic matter respiration in intermediate depth waters (Expedition 323 Scientists, 2011). Thus, past changes in the strength and extent of the BSC due to changes in the amount of sea ice and circulation, as well as any associated variations in the OMZ could significantly impact the benthic communities below.

Pleistocene Climate and Bering Sea Paleoceanography

The Mid-Pleistocene Transition (MPT) corresponds to the period between ~1.25 and 0.7 Ma (Elderfield et al., 2012) when Milankovitch orbital cycles shifted significantly from the 41-kyr cycles (obliquity) that dominated the early Pleistocene to 100-kyr cycles (eccentricity) in the late Pleistocene. During this transition, climate

variability and northern hemisphere ice formation expanded, resulting in more intense glacial conditions and longer transitions between glacial and interglacial periods. Changes in glacial cycles during the Pleistocene altered oceanic circulation, nutrient delivery, and sediment supply to the sea floor (Takahashi, 2005).

Conditions such as shorter and colder summers, increased spatial extent of sea-ice cover, low salinity melt water cover, and restricted supply of sub-surface nutrients to the surface layer (less upwelling due to hindered convection) have been associated with the Last Glacial Period (Cook et al., 2005; Kim et al., 2011). Additionally during the Last Glacial Period, perennial to semi-perennial sea ice is thought to have extended past the shelf edge over the slope in some areas of the Bering Sea (Kim et al., 2011; Asahi et al., 2015). Glacioeustatic sea level drop during the LGM is interpreted to have weakened or cut off the supply of warm Alaskan Stream waters over the Bering Slope sites from the shallower passes and diverted the flow westward through the deeper Aleutian passes (Katsuki and Takahashi, 2005).

Because of the counter-clockwise surface flow patterns, this would have promoted more sea ice formation and created less favorable conditions for warm water diatom blooms (Expedition 323 Scientists, 2011). Sea ice melting near the shelf edge brings large numbers of diatoms to the sea floor (Alexander and Niebauer, 1981), which were likely the primary food source for benthic organisms during deglacial periods. Additionally, repeated sub-aerial exposure of the Bering Strait and partial exposure of the existing shelf is likely to have resulted in much different circulation and sedimentation patterns during glacial time periods (Expedition 323 scientists, Site

U1344, 2011). These alternating environments resulted in large quantities of diatoms being deposited during warm periods, in contrast to times of glacially lowered sea level and riverine incision into the shallower shelf, which would have brought more coarse sediment to the slope area (Aiello and Ravelo, 2012).

MATERIALS & METHODS

IODP Expedition 323 and Site U1344

Seven sites (U1339 to U1345) distributed on a depth transect ranging from 819 to 3173 m below sea level (mbsl), and covering three different regions in the Bering Sea (Umnak Plateau, Bowers Ridge, and the Bering Slope region), were cored successfully during IODP Expedition 323. This study focuses on the deepest site, Site U1344 (59°3.0'N, 179°12.2'W), located on a canyon interfluve on the northern lower slope of the Aleutian Basin at 3173 m water depth. The location of Site U1344 is in an area proximal to the gateway to the Arctic Ocean and is subject to a high amount of terrigenous sediment input from the Russian Anadyr River and the Alaskan Yukon River (Takahashi et al., 2011). The site lies well below the present day OMZ, and is currently the coldest (bottom water temperature: <2°C) and most oxygenated (dissolved oxygen >2ml/L) among the sites cored during Expedition 323 (Expedition 323 Scientists: Site U1344, 2011, Figure 3).

Five holes were cored at Site U1344 to various depths below the seafloor (Takahashi et al., 2011). This study centers on the deepest hole (U1344A) that extends from the seafloor down to 746.6 mbsf. Total core recovery in Hole U1344A was 648.1m or 87% of cored interval (Takahashi et al., 2011). The sedimentary record at Site U1344 consists of a mix of terrigenous, glaciomarine, and biogenic components. Terrigenous sediment is mostly composed of angular siliciclastic and volcaniclastic grains. Biogenic sediment consists mostly of diatoms and radiolarians, and to a much lesser degree

calcareous nannofossils, foraminifera, and ostracods (Takahashi et al., 2011; Aiello and Ravelo, 2012; Alvarez Zarikian, 2016). The sediment cores obtained from Site U1344 contain more pelagic clay than any other Expedition 323 site, owing to its deep slope edge location (Aiello and Ravelo, 2012). The presence of benthic foraminifera combined with moderately good carbonate preservation and high sediment accumulation rates make Site U1344 suitable for reconstructing bottom water environmental conditions.

Age Model

The chronostratigraphic framework for Site U1344 is based on biostratigraphic datums and magnetostratigraphic data (chron ages) primarily obtained from shipboard analyses during Expedition 323 (Takahashi et al., 2011; Lund et al., 2016). Linear interpolation of these data provide estimated sediment accumulation rates ranging from ~30 to 90 cm/ky, with an average of ~45 cm/ky, throughout the sequence (Expedition 323 Scientists, 2011: Site U1344; Figure 4).

Laboratory Sample Processing

For this study, 276 samples were taken at a resolution of 2-4 samples per core (a core is usually ~9.5 m long, but the length may vary depending on core recovery) throughout the entire cored interval in Hole U1344A, and examined for benthic foraminifera. An average sample spacing of 3 m provided a temporal resolution of ~7 ky based on the shipboard age model and average sedimentation rate of 45 cm/ky (Takahashi et al., 2011). Sediment sample volume was ~34 cm^3, which is equivalent to a

2 cm half-round core sample. Samples were oven-dried at 50°C, weighed, washed with distilled water over a 63-µm sieve, and then the sand fraction was oven-dried at 50°C and weighed. The sand fractions (>63 µm) were later dry-sieved using a 125 µm mesh for examination, and all benthic foraminifers in this size fraction were picked, identified and counted using a light microscope.

Taxonomic Analyses

Benthic foraminifera were identified primarily utilizing studies from the North Pacific, the Bering Sea, and Arctic regions and following the taxonomic works of Keller (1980), Ohkushi et al. (2000), Saidova (1961), and Setoyama and Kaminski (2015). Many of the species that occur at Site U1344 are common in nearby marginal seas (Sea of Japan, Okhotsk Sea) and the Northwest Pacific Ocean (Saidova, 1961; Keller, 1980; Kato, 1992; Okhushi et al., 2000; Bubenshchikova et al., 2008). Benthic foraminifera were characterized by total abundance (total number of specimens per sample) and the relative abundance of individual taxa. Diversity patterns were determined by the species richness (total number of species, *S*) and the Simpson Index (D):

$$D = 1 - (\frac{\sum_{i=1}^{S} n_i}{N(N-1)}),$$

where n_i = total number of specimens of species i, and N = total number of specimens of all species.

Benthic Foraminifera Accumulation Rate (BFAR) as a Proxy for Paleoproductivity

To reconstruct paleoproductivity, benthic foraminifera accumulation rates (BFAR) were calculated following the methods of Herguera and Berger (1991). The Benthic Foraminifera Accumulation Rate (BFAR) is expressed as the number of benthic foraminifera per centimeter squared, per thousand years, and is calculated by the following equation:

$$BFAR\,\frac{BF}{cm^2 kyr} = (\,BF \times LSR \times DBD),$$

where *BF* = number of benthic foraminifera per 1 gram of sediment, *LSR*=linear sedimentation rate (cm/kyr), *DBD*= dry bulk density (g/cm^3) (Herguera and Berger 1991; Diaster-Hess et al., 2011). Values produced are interpreted to be an indirect measure of paleoproductivty, based on the principle that one benthic foraminifer shell is deposited for every 1 mg of organic carbon fluxed to the sea floor (Herguera and Berger, 1991).

Statistical Analyses and Comparison with Other Sites

Statistical analyses were implemented in this study to determine inter-species relationships, identify assemblages, and highlight patterns of change through time. Genus-level relative abundance matrices were generated for Site U1344, and also for nearby Site U1343 (at 1953 mbsl). Benthic foraminifera counts from Site U1343 were provided by Dr. Sev Kender from the British Geological Survey. Only genera making up 1% or more of the total were included (from both sites, combined) in order to reduce the influence of rare taxa. Analysis of data including all taxa (and with a more generous

0.5% cutoff) produced a large amount of statistical noise due to rare and sporadic appearances of some taxa. Furthermore, the incorporation of additional, rare species did not alter the relationships among the most dominant taxa.

Cluster analysis was utilized as a tool for grouping species into assemblages interpreted to have similar ecological preferences. Taxon clusters were generated for benthic foraminifera from Sites U1344 and U1343 individually, as well as for the combined data set. The cluster analysis was implemented in the R statistical computing environment using the Vegan 2.0 library (Oksanen et al., 2015). Clusters were created using average linkage clustering and the Bray-Curtis similarity metric (Legendre and Legendre, 2012). These dendrograms were used to create two-way cluster analyses which allow taxonomic groupings to be related to sample groupings. These sample groupings represent genera with similar abundance records.

A principal coordinates analysis (PCO) was implemented on the benthic foraminifera data from Sites U1344 and U1343 to compare the two fossil records and assemblages to one another. Site U1343 was incorporated in order to compare and contrast two records with a similar time range and relatively close locations, to increase the robustness of the method, and better understand the depth-correlated ecological gradient in the Bering Sea benthic communities. The records from Sites U1343 and U1344 are readily comparable because these sites are geographically close to one another (110 km apart) on the Bering Slope (although Site U1344 is 1247 m deeper), and they cover approximately the same time interval (Site U1344: ~1.9Ma, Site U1343: ~2.4Ma, Figure 4). Due to their difference in water depth, the sites have slightly different

physiochemical characteristics (Takahashi et al., 2011; Figure 3). Starting with a Bray-Curtis dissimilarity matrix (calculated using vegdist {vegan} in R), a PCO was conducted using FSP (flexible shortest paths or extended dissimilarities) with a "too long" parameter of 0.9 (De'ath, 1999). This method helps mitigate artifacts in ordination results arising from large variations in species composition among samples. The final PCO was generated using the function capscale{vegan} (Legendre and Legendre, 2012).

RESULTS

Downhole Records of Benthic Foraminifera at U1344

A total of 16,495 benthic foraminifers belonging to 59 taxa were picked, counted and identified. Taxa were largely identified to species level, although in a few cases, only to genus level identification was possible. Benthic foraminifer abundance ranges from 0 to 959 specimens per sample (sample mean 60). Sixty-four samples (23%), mostly concentrated in the bottom half of the record, were barren. Ten samples yielded substantial abundance peaks of over 400 specimens (seven of these in the upper 300 m CCSF). Preservation ranges from poor (shells are abraded, opaque, brownish/yellowish, dissolved or recrystallized) to excellent (shells are pristine, translucent). Average density per gram is 18, the sample median is 54, and the mean is 45 specimens. Most of the species found at Site U1344 are found at other Bering Sea sites (Takahashi et al., 2011; Setoyama and Kaminski, 2015), and are also common in the Okhotsk Sea (Khusid et al., 2005; Bubenshchikova et. al., 2008) and the North Pacific.

The most commonly occurring benthic foraminifera at Site U1344 are *Elphidium* spp. (42% overall, with *E. batialis* as the most abundant species) and *Valvulineria sadonica* (13% overall). These are followed by *Eubuliminella exilis* (*Bulimina exilis* in Keller 1980 and Okhushi et al. 2000), *Uvigerina* spp. *(U. senticosa* and *U. yabei)*, *Evolvocassidulina tenuis*, *Nonionellina labradorica*, *Melonis pompilioides*, *Globobulimina* spp. *(G. auriculata*, *G. pacifica,* and *G. affinis), Cibicidoides* spp. (*C. mundulus* and *C. lobatulus*), *Gyroidina* spp., and *Lagena* spp. All the major taxa

collectively represent >94% of the total assemblage, and each of the genera in the second group range from 1 to 8.7%overall. In terms of stratigraphic range, *Elphidium*, *Valvulineria*, *Nonionellina*, *Melonis*, *Cibicidoides*, *Evolvocassidulina*, and *Globobulimina* are present periodically throughout the entire record, with *Elphidium* and *Valvulineria* showing an inverse correlation in relative abundance through the core. In contrast, *Uvigerina* and *Eubuliminella* are found only in the upper half of the cored interval with their first occurrences observed during the late part of the Mid-Pleistocene Transition (at ~0.9 Ma for *Eubuliminella* and ~0.8 Ma for *Uvigerina*) (Figure 5). *Cibicidoides* is common at this site although it is absent or nearly absent from all other Expedition 323 sites (Takahashi et al., 2011).

The benthic foraminiferal abundance, diversity, and benthic foraminifera accumulation rates (BFAR) show general increasing trends from the base of the record to ~650ka and a more steady average during the late Pleistocene, although many maxima and minima characterize the records (Figure 6). Six major peaks in absolute abundance (>100 specimens/g) are observed at ~1.25, 1.0, 0.65, 0.6, 0.4 and 0.1 Ma (Figure 6) and they usually correspond to spikes in *Elphidium* populations. The basal part of the record (from ~1.9 to ~1.2Ma) produced the lowest concentrations of benthic foraminifera (average 28 per sample) and many barren samples.

Elphidium makes up to 67% of the early Pleistocene assemblage, while *Valvulineria* predominates from 1.5Ma to 0.9Ma. Apart from *Valvulineria* and *Elphidium*, deep infaunal taxa are the most common type at Site U1344 but their relative abundance varies; several extended periods of decreased relative abundance of this

group are observed around ~1.3Ma, 0.95Ma, and 0.6 Ma (Figure 6). Benthic foraminifera that belong to the deep infaunal group at Site U1344 include *Globobulimina*, *Evolvocassidulina*, *Nonionellina*, and *Eubuliminella*.

Through the MPT, benthic foraminifera abundances increase to an average of ~50 specimens per sample and the assemblage becomes dominated by more elongate, low oxygen, deep infaunal types. Diversity also increases (and now includes *Eubuliminella* and *Uvigerina*) indicating that conditions became more favorable for benthic foraminifera at Site U1344. Near the end of the MPT, some of the highest densities of benthic foraminifers are found. Overall, the late Pleistocene displays the greatest abundance (average of 97 specimens per sample) and BFAR of benthic foraminifera.

Assemblage Clusters

Statistical clusters were generated in order to determine similarities between genera and to define foraminiferal assemblages using the most common taxa at Site U1344, and also at U1343. The most common genera present at Site U1344 are also commonly found at Site U1343, with the exception of *Melonis pompilioides*, which is not present at U1343, *Gyroidina* sp., which is extremely rare at Site U1343 but common at U1344, and *Islandiella norcrossi*, which is abundant at Site U1343 but rare at U1344. Five groupings are defined in the cluster dendrogram in Figure 7, using the combined data sets from Sites U1344 and U1343, which collectively include 13 genera. Clusters are interpreted to represent assemblages of foraminifera with similar distributions among

samples. Their downhole trends (plotted in Figure 8) show that some assemblages fluctuate regularly throughout the entire cored interval (Assemblages II and V), while others increase to their highest abundances or make their first appearance during the MPT (Assemblages I and III), suggesting environmental changes through time implied by the large differences in assemblage dominance and composition between the early and the late Pleistocene.

Principal Coordinates Analysis of Benthic Foraminifera at Sites U1343 and U1344

The principal coordinates analysis (PCO) conducted on the combined data set (a single relative abundance matrix including data from both U1343 and U1344) is presented in Figure 9. This analysis aims to draw out information related to environmental factors affecting the benthic foraminiferal assemblages, as well as to highlight similarities and differences in the distribution of benthic foraminifera within and between Sites U1343 and U1344. Sample scores for U1343 and U1344 are segregated based on generic composition. Sample scores for U1344 spread out laterally along axis one, while the scores for Site U1343 are primarily distributed along axis two. The two sites overlap in samples where *Elphidium* is dominant and both sites appear to show distribution of samples along faunal gradients. These gradients diverge from the *Elphidium*-dominated samples towards *Islandiella* and *Epistominella* in the case of Site U1343, and towards *Valvulineria*, *Melonis*, and *Globobulimina* for Site U1344. The partitioning of scores based on assemblage composition at each site suggests differences in environmental conditions between the two sites. Where they overlap, species common

to both sites are displayed (Assemblage I and III: *Nonionellina*, *Evolvocassidulina*, *Uvigerina*, *Eubuliminella*).

The PCO sample scores were plotted against sample age in order to visualize shifts in assemblage composition through time (Figures 10 and 11). The variation of Site U1344 is most evident along axis 1 when plotted versus age (Figure 10A). The earliest part of the record shows overlap of both cores, indicating similar benthic assemblages (driven by high abundance of *Elphidium*) until about 1.5 Ma. From ~1.5Ma to 0.8 Ma the two curves diverge, indicating a more substantial environmental difference between the two cored site locations than before 1.5Ma. At this time in Site U1344, *Elphidium* decreases and *Valvulineria* becomes more dominant. After 0.9Ma, the cores become more similar as *Elphidium* becomes more dominant in the assemblage. They diverge again around 0.5Ma to the present, as *Elphidium* declines and the assemblage shifts back to dominance by *Valvulineria*.

Axis 2 versus age (Figure 10B) shows less overlap between the two sites, and much less variation is observed for Site U1344, which indicates that the benthic assemblage at U1343, (and those reflected by this axis), was not responding in the same way as U1344. Site U1343 shifts to a more similar state to U1344 from 1.5-1.2 Ma, and 0.8-0.6 Ma (driven again by high numbers of *Elphidium*) and is most different from U1344 at 1.9 and 1.0 Ma – representing the dominance of *Islandiella* at this site during those times.

DISCUSSION

Environmental Preferences of Dominant Species at U1343 and U1344

A significant portion of the assemblages at both sites is composed of deep infaunal taxa, which are tolerant of lower oxygen conditions and are often associated with increased surface productivity and high organic matter flux to the sediment (Corliss, 1985; Khusid et al., 2005). At the same time, Site U1344 also shows the highest concentrations of shallow infaunal and epifaunal taxa (e.g., *Cibicidoides* and *Gyroidina*) among the Expedition 323 sites. Many of these planoconvex to biconvex taxa have been described from well-oxygenated environments, although observations of these taxa in hypoxic environments suggest that they probably are less sensitive to low oxygen, and rather prefer sediment surface habitats for their dependence on a supply of high quality food particles (Jorissen et al. 2007).

The three most common species at the two sites: *Elphidium* (*E. batialis*), *Valvulineria* (*V. sadonica*), and *Islandiella* (*I. norcrossi*) are common to other areas in the North Pacific and their modern day environmental distribution can be useful for interpreting changes in the studied interval. In living populations from the Okhotsk Sea, *E. batialis* was found to be most abundant at sample locations under generally sea ice-free surface conditions, bottom waters where oxygen levels were relatively high (1.0-2.0 ml/l), and food supply was abundant. Moreover, *E. batialis* has been reported from highly productive regions in the North Pacific, including slope sites in the Aleutian and Komandor Basins in the Bering Sea, near Hokkaido and Honshu Islands, and in the

Kurile–Kamchatka Trench (Saidova, 1961; Khusid et al., 2005, 2006). In Khusid et al. (2005), *Elphidium* is described as detritophagous (feeding on phytodetritus) and thermophilic (preferring warmer water). *Elphidium batialis* has been found to be most abundant during warm periods (the Holocene and MIS 5e) in a late Pleistocene record from the Okhotsk Sea (Khusid et al., 2005).

Valvulineria sadonica has been described as an intermediate to deeper infaunal species that thrives under high and sustained flux of degraded and refractory organic matter and is tolerant of suboxic to high oxic conditions (Bubenshchikova et al., 2015). *V. sadonica* has been associated with an expanded OMZ in the Okhotsk Sea (Bubenshchikova et al., 2015) and has also been observed to characterize foraminiferal assemblages during warm climate periods (Khusid et al., 2005). Like *V. sadonica*, other *Valvulineria* species also have been associated with regions with high organic matter accumulation. In the Mediterranean region, previous studies have evidenced correlation between *Valvulineria bradyana*-dominated assemblages and high organic flux of fluvial (terrigenous) origin (Bergamin et al., 1999; Frezza et al., 2005). The largest difference between *Valvulineria* and *Elphidium* therefore could be food preference, (quality of organic matter), although lower oxygen could be a potentially limiting factor for *Elphidium* as well.

Islandiella (*I. norcrossi*) is also a shallow infaunal phytodetritivore and is associated with seasonal surface productivity (Knudsen et al., 2012; Bubenshchikova et al., 2015). However, in the Okhotsk Sea, it was found in highest abundance at locations with high sea ice concentrations (often >75% and lasting up to 6 months of the year),

oxygen levels 0.5-1.0 mL/L, and where the flux of organic matter was lower than where *Elphidium* was dominant (Bubenshchikova et al., 2008). Khusid et. al (2005) observed *I. norcrossi* (*Cassidulina teretis* in their study) to be dominant in glacial assemblages and reduced during warm periods and furthermore, describe this species as highly resistant to unfavorable conditions (such as reduced productivity) which accompanied glacial periods. As *E. batialis* and *I. norcrossi* have both been described as a phytodetritovores, food type is not as likely to be a factor distinguishing these two species at Site U1343.

Additional species from Site U1344 can be considered as higher productivity indicators or are associated with flux of more fresh and labile organic matter. Several studies observe *N. labradorica* as occurring in time periods also characterized by high numbers of *Elphidium* (Khusid et al., 2005; Bubenshchikova et al., 2008; Balenger et al., 2016), implying that these two species occupy or tolerate similar environments in the North Pacific. Additionally, *N. labradorica* has been described as feeding on fresh phytodetritus and is associated with high seasonal surface productivity (Knudsen et al., 2012), and is therefore most similar to *Elphidium* and *I. norcrossi* in that way. *Eubuliminella (E. exilis)*, is an elongate deep infaunal species characteristic of increased and sustained organic matter flux, and peaks when there is input of fresh, labile organic matter (Caralp, 1989). *Uvigerina* has also been found to be abundant under high continuous input of fresh organic matter (Ohkushi et al., 2000; Lutze & Coulbourn, 1984).

Alternatively, *Cibicides* (*C. wuellerstorfi*), *Gyroidina* (*G. altiformis* and *G. orbicularis*) are found almost exclusively below 2.5g/m^2/year flux rates (Altenbach et

al., 1999), and in live populations from the Okhotsk Sea, *G. orbicularis* (the most common species of *Gyroidina* present at Site U1344) was found at sites with the lowest annual organic carbon flux rates (at the same sites as *I. norcrossi)* (Bubenshchikova et al., 2008). These groups therefore, may also be advantaged over some others when flux levels are lower. High relative abundance of the deep infaunal dwelling *Globobulimina* is observed at Site U1344; this species has been described as not necessarily requiring fresh organic material and rather relying on degraded, refractory, and residual organic matter within the sediments (Alve, 2010). Some species of *Melonis* (*M. barleeanus*) are found to be most abundant when available organic matter is more refractory as well (Caralp, 1989), making these groups more similar to *Valvulineria* in terms of associated feeding habits and environmental tolerance. The distinction between which groups require more fresh organic matter versus relying on more degraded or refractory organic matter provides a context for which to interpret the benthic foraminiferal assemblages in the Bering Sea slope sites over the last 2 Ma.

Benthic Foraminiferal Composition at Site U1344 Through the Pleistocene

Glacial-interglacial cycles are among the most prominent environmental signals anticipated in the Quaternary fossil record. This is especially true for Site U1344, given its proximity to the Northern Hemisphere ice sheets, its high latitude, and the semi-enclosed nature of the Bering Sea. However, records of benthic foraminifera from Site U1344, even at a resolution of ~6400 years, do not appear to strongly reflect this signal.

The most prominent changes in benthic foraminiferal assemblages at Site U1344 take place during the mid-Pleistocene (Figures 5, 6, 8), when some taxa become significantly less abundant (e.g., *Gyroidina*, *Lagena*), while others become very abundant or appear in significant numbers of for the first time in the record (e.g., *Eubuliminella*, *Uvigerina*). These shifts in the benthic foraminiferal populations likely reflect environmental changes across the Mid-Pleistocene Transition that are likely related to the intensification of northern hemisphere glaciation . The largest observable shifts in the benthic foraminifer record at Site U1344 likely reflect changes in surface productivity, quantity and type of food (e.g. phytoplankton flux vs. terrigenous organic matter) to the bottom sediments, and/or bottom water circulation changes that may have resulted from glacial intensification. Recent studies have shown significant cooling of the Bering Sea starting during the MPT: Teraishi et al. (2013) and unpublished data from Site U1344 (Stroynowski, personal communication) show an abrupt decrease in the abundance of warm water diatom species (indicative of Alaskan Stream water) around 0.9 Ma, accompanied by an increase in neritic diatom species (indicative of more coastal-like conditions and thus, lowered sea level near the slope sites) and an increase in sea ice diatoms (first around 1.25 Ma and consistently high after ~0.9 Ma). Iwasaki et al. (2015) reported decreased export production at Bowers Ridge Site U1341 beginning at 0.85 Ma, which was also accompanied by an increase in sea ice diatoms. Asahi et al. (2016) suggest that sea ice expanded past the shelf (and over the Expedition 323 slope sites) after 0.9 Ma based on significantly lowered sedimentation rates and increased magnetic susceptibility, which are both indicators of glaciomarine sedimentation.

Decreasing biogenic opal was also reported from Site U1343, starting at 1.9 Ma and dropping significantly at 1.25 Ma and 0.9 Ma (Kim et al., 2014).

These records imply intensification of glacial intervals affecting Sites U1344 and U1343 during and after the MPT that resulted in changes in the quantity, quality, and type of food (e.g. diatoms) available to the benthic biota. The overall benthic foraminiferal diversity and abundance of deep infaunal species increased at Site U1344 through the MPT, and the first occurrences of *Eubuliminella* (*E. exilis*) and *Uvigerina* spp. occur near the end of the MPT. The appearance of these two species suggests that productivity increased and the flux of fresh organic matter became more sustained in the post-MPT part of the record.

Comparison of Benthic Foraminiferal Assemblages at Sites U1344 & U1343

Sites U1343 and U1344 are located along the slope edge near submarine canyons and subject to delivery of a large amount of both terrigenous and biogenic material. In addition, both sites are located under the path of the Bering Slope Current and are near the edge of seasonal sea-ice extent. The main difference between Sites U1343 and U1344 is their depth (1900mbsl and 3200mbsl, respectively), their position within the oxygen minimum zone (OMZ), and the water masses they are bathed in. Site U1343 is situated on a bathymetric high and semi-isolated from the slope around it. It is also presently near the deep edge of the OMZ and therefore more likely to be experience fluctuations in dissolved oxygen resulting from changes in the strength and extent of the OMZ. Site U1344 is well below the present OMZ and is less likely to be affected by

changes in its intensity or depth range (although changes in dissolved oxygen could occur at U1344 with changes in deep water circulation and burial rate of organic matter).

Most of the benthic foraminifera present at Sites U1343 and U1344 are associated with high productivity and low oxygen. However, they differ in the dominant taxon: *Islandiella* is dominant at Site U1343, but extremely rare at U1344, whereas *Valvulineria,* is found in higher numbers at Site U1344. *Elphidium* predominates at both sites. The overall segregation of samples from U1343 and U1344 in the PCO (Figure 9) suggests that the two sites reflect different bottom water environmental conditions and experienced a different history of change through the study interval. The samples from the two sites that are most similar are the ones that are dominated by *Elphidium*, which defines one end-member of the species gradient at both sites.

For Site U1344, the primary species gradient varies from *Elphidium* to cluster Assemblage I (*Nonionella*, *Evolvocassidulina*, *Uvigerina*) to cluster Assemblage II (*Melonis*, *Valvulineria*, *Cibicidoides*, *Globobulimina*) and *Valvulineria* (on the far right of the plot; Figure 9). *Elphidium* is commonly associated with well-oxygenated conditions that have ample fresh organic matter delivered from surface waters, while Assemblage I is mostly made up of foraminifera that prefer a sustained supply of fresh organic matter. Groups that cluster with *Valvulineria* in the PCO cross plot, (*Globobulimina*, *Cibicidoides*, *Melonis*, *Gyroidina*) are considered indicative of highly degraded, refractory or residual organic matter and potentially lower organic matter flux rates. Based upon theses associations, variation along PCO axis one most likely reflects changes in the quality and type of organic matter reaching Site U1344 over time.

Groups that cluster on the *Valvulineria*-end member at Site U1344 (Assemblage II and *Gyroidina*) are extremely rare in presence at Site U1343, which suggests that Site U1343 received less degraded and refractory organic matter than Site U1344. This is to be expected as U1344 is deeper and subject to a larger amount of "leftover" material as surface-produced organic matter is consumed at intermediate and shallower depths as it sinks to the sea floor. In addition, the association of the shallow infaunal to epifaunal species *Melonis*, *Cibicidoides*, and *Gyroidina* with well-oxygenated environments may help explain their relatively low abundance at Site U1343 as dissolved oxygen are expected to be stably higher at Site U1344 than at U1343 (due to position of the OMZ).

The primary species gradient in U1343 is from *Elphidium* to the high productivity group (Assemblage II: *Eubuliminella, Nonionella, Evolvocassidulina*), to *Islandiella*. The largest difference between the two dominant species is that *Elphidium* often requires large amounts of surface productivity, whereas *Islandiella* has been reported as surviving under low organic matter flux (Khusid et al., 2005). *Eubuliminella* is associated with elevated and sustained flux of fresh, labile organic matter but is also tolerant of very low oxygen concentrations, suggesting that it occupies an ecological niche that is not preferentially exploited by either *Elphidium* (high labile organic matter but with high oxygen) or *Islandiella* (low organic flux and low oxygen).

Overall, the scatter of sample points from each site appear to reflect a gradient in the amount and/or quality of organic matter delivered from surface waters, but under different oxygen concentration regimes. Site U1343, the shallower site, is near the edge of the OMZ and is therefore expected to experience lower oxygen levels than U1344,

which is below the OMZ and bathed in oxygenated oceanic deep water (Figure 3). At each site, there appear to be times when relatively fresh, labile organic matter reached the sea floor (dominated by *Elphidium*) and times when it did not (dominated by *Islandiella* at U1343 and *Valvulineria* at U1344), perhaps reflecting changes in surface conditions where the organic matter is produced, with *Elphidium* representing times of high productivity and the opposite end-member of the species gradient reflecting times of low productivity under different benthic oxygen conditions.

The segregation of samples from site U1343 and U1344 based on species composition seen in the PCO (Figure 9) indicates that the two sites reflect differing environmental controls on the benthic foraminiferal assemblages. The changes at the two sites through time were not concurrent. Variations in factors like oxygenation and organic matter quality are likely to be strongly driven by expansion or melting of sea ice, but more information is needed to tie sea-ice concentration to fluctuations in the benthic community confidently, the way diatom proxy records are for Site U1344.

Environmental Change Through the Pleistocene at the Bering Slope Sites

Plotting PCO scores against age (Figure 11) provides a way of picturing how foraminiferal composition changed over time at the two sites. At site U1344, changes through time represent the shift in dominance from *Elphidium* to *Valvulineria* (captured on PCO axis 1, Figure 11A), and at site U1343, changes through time represent the shift in dominance from *Elphidium* to *Islandiella* (PCO axis 2, Figure 11B). Based on species' reported environmental preferences, times when the foraminiferal community

was at the *Elphidium*-dominated end of the species gradient are considered times of high surface productivity.

Variation at Site U1344 over time is interpreted to reflect the quality of organic matter as the assemblage shifts in dominance from *Elphidium* to *Valvulineria* over time. This association suggests that before the onset of the MPT (~1.5Ma) higher amounts of refractory and degraded organic matter were available at Site U1344, until about 0.9Ma, when the primary food source switched to include more fresh organic matter. A small excursion back to the *Valvulineria*-end of the gradient is observed at ~0.4Ma, but does not extend into the present as the data trends towards the *Elphidium* end of the gradient in the top (most recent) part of the record.

The shifts in the PCO curve versus age for axis two could represent changes in oxygenation of the bottom waters or strength and position of the OMZ near Site U1343. If the variation along this axis does reflect oxygen, then the shifts of the U1343 PCO curve towards the *Islandiella*-end of the gradient that are observed at ~2.4, 1.9, and 1.0 Ma (Figure 11), could represent times when the lower boundary of the OMZ because deeper and lower dissolved oxygen limited *Elphidium* but was advantageous for *Islandiella.*

Based on trends along both PCO axis (Figure 11), from 2.0 to 1.5Ma there was generally lower oxygen at Site U1343 (*Islandiella*-dominated) but higher fresh organic matter reaching Site U1344 (*Elphidium*-dominated). Samples from the interval from ~1.8 to 1.5 Ma are barren at site U1344 but not at Site U1343, suggesting that an event occurred at the deeper site that did not affect Site U1343. There is insufficient

information to determine whether the prominent absence of benthic foraminifera at Site U1344 represents harsh bottom conditions in the deeper waters during this time or is a result of destructive post-depositional processes. At this time at Site U1343, the assemblage appears to be relatively stable as the PCO curve shows relatively little variation toward either end of the environmental gradient. After 1.5 Ma, Site U1344 becomes characterized by high dominance of *Valvulineria* (until ~0.9Ma). The decrease in dominance of *Valvulineria* could be a result of potentially higher competition driven by increased flux of fresh, labile organic matter and phytodetritus as evidenced not only by higher dominance of *Elphidium*, but also following the first appearances of *Eubuliminella* and *Uvigerina* around this same time.

The trend observed for Site U1343 on PCO axis 2 across the MPT suggests oxygen levels increasing (represented by maximum abundance of *Elphidium* at ~1.3 Ma) then decreasing strongly until 0.9Ma. Both sites therefore, appear to show this sharp shift around ~0.9Ma, which is recorded by many proxy records derived from the Bering Sea Expedition 323 studies. Through the late Pleistocene, the PCO plots for the two sites appear to shift similarly, but while the benthic foraminiferal assemblage appears relatively stable at Site U1343, a large shift to poorer organic matter quality (or potentially more limiting oxygen levels for *Elphidium*) is observed around 0.4Ma for Site U1344.

CONCLUSIONS

Studies of the Bering Sea have been limited and research presented from Expedition 323 sites has greatly enhanced understanding of changes in Pleistocene paleoceanography and how surface to benthic connections were altered with the onset of Northern Hemisphere glaciation during the Pleistocene. The objective of this study was to analyze the benthic foraminiferal record from IODP Site U1344 (the deepest site drilled during Expedition 323), in order to understand the oceanographic and paleoecological history of the deep Bering Sea and factors affecting the benthic environment over the last 1.9 Ma. The strongest signal in the data at U1344 does not appear to be the glacial-interglacial cyclicity that is characteristic of much of the Quaternary record; a higher sample resolution is needed to tie the fossil record to specific intervals. Rather, diversity and abundance of benthic foraminifera increased at Site U1344 through the Mid-Pleistocene Transition, despite gradually declining biogenic opal flux near the slope sites during this time period. The benthic foraminferal assemblage shifted to include more deep infaunal and higher productivity groups in the later part of the record, which suggests that a sustained supply of fresh, labile, and particulate organic matter became more available to the benthic communities after the MPT.

The dominant genera of benthic foraminifera at U1344 (*Elphidium* and *Valvulineria*) and Site U1343 (*Elphidium* and *Islandiella*) are interpreted to fluctuate over time in response to changes in food quality and type and also potentially in oxygen.

In the context of the PCO plots at the Bering Slope sites, it appears that *Elphidium* represents conditions when phytodetritus was abundant; at the opposite end of the ecological gradient at U1343, *Islandiella* represents the lower oxygen, whereas at the opposite end of the ecological gradient at U1344, *Valvulineria* represents decreased quality of food. Both Sites appear to have recorded a large shift toward *Elphidium*-dominated communities around ~0.9Ma, which is consistent with several other proxy records derived from IODP Expedition 323 studies. The changes in assemblages of benthic foraminifera that occur over the last ~2.0Ma at Site U1344 cannot be simply explained by increased sea ice cover and decreased productivity as most groups present after ~0.9Ma represent higher productivity and more fresh and sustained flux of organic matter. Although the influence of dissolved oxygen is less straightforward in the benthic foraminiferal data, interpretation of the assemblages from the Bering Slope sites suggests that benthic foraminifera at Site U1343 vary as a function of changes in bottom water oxygenation and/or variation of the oxygen minimum zone, while benthic foraminifera at Site U1344 most likely reflect changes related to food supply, source, and quality.

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APPENDIX: FIGURES

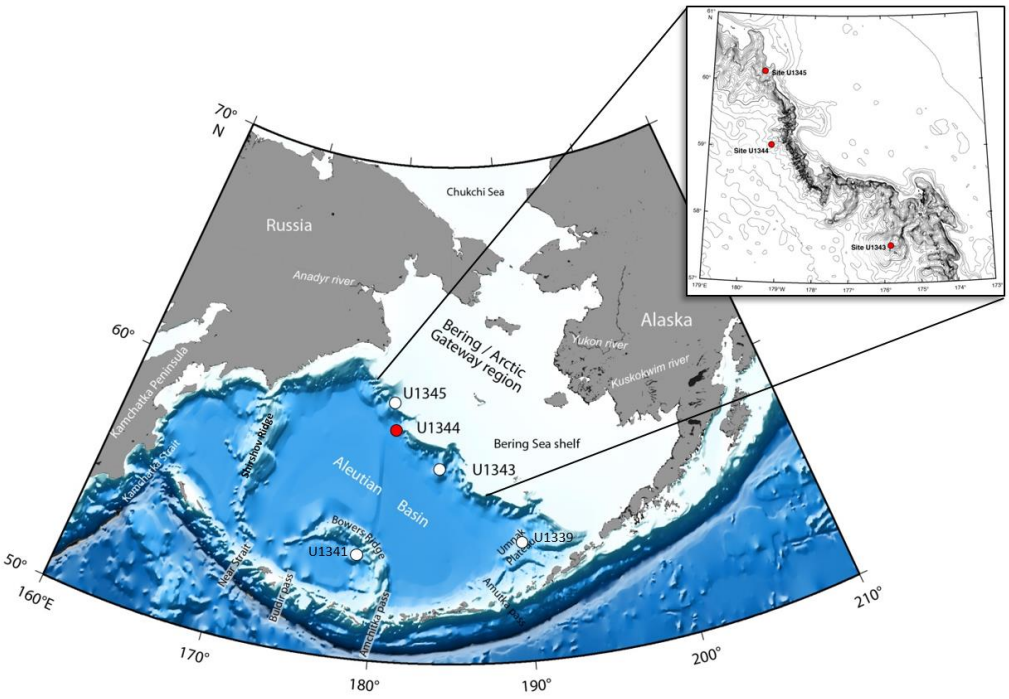

Figure 1: Map of the Bering Sea with Site Locations. Expedition 323 Slope Sites: U1344 (indicated in red), U1343 and U1345.

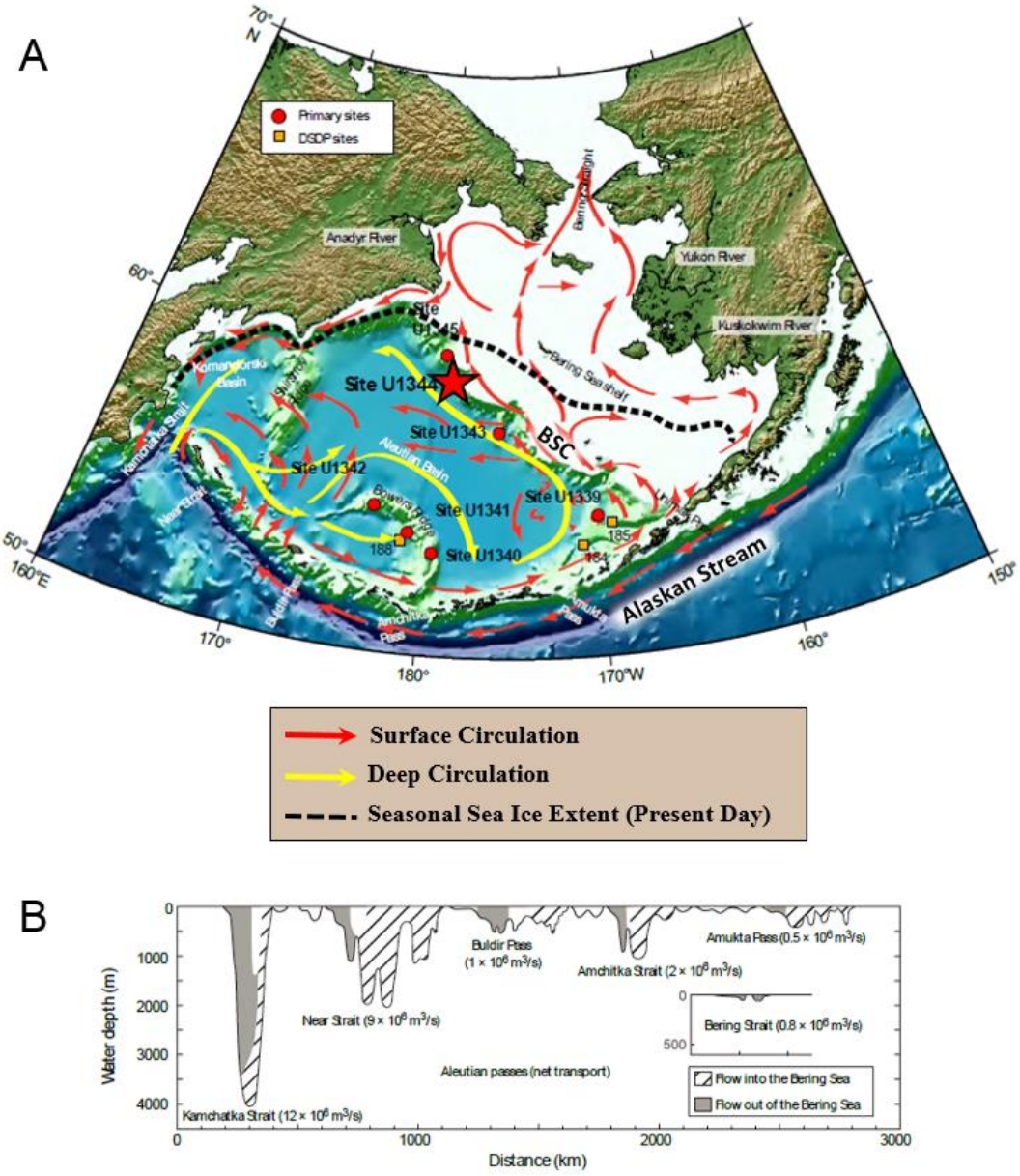

Figure 2: Map of the Bering Sea with Ocean Circulation Patterns.
A: Map with deep (red) and surface (yellow) circulation patterns. Seasonal sea ice extent indicated with dotted line (modified from Aiello and Ravelo, 2012).
B: Cross-sectional view of flow patterns through the Aleutian passages and the Bering Strait (adapted from Takahashi, 2005).

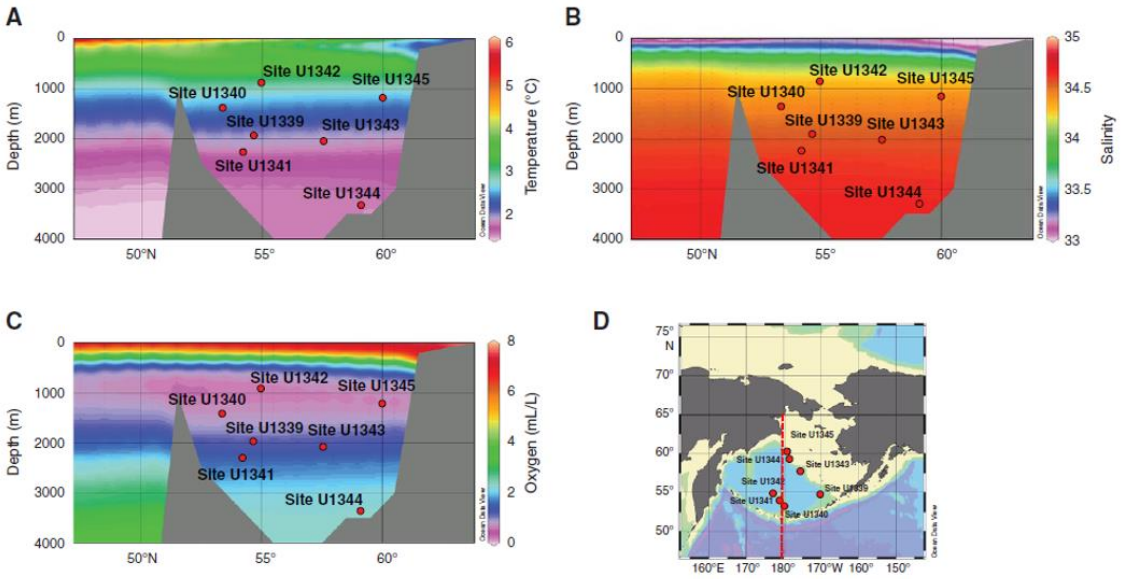

Figure 3: Modern Physiochemical Properties of the Bering Sea. Cross-sectional views of relative position for Sites from Expedition 323 are plotted versus present-day A. Temperature (A.), Salinity (B.), and Dissolved Oxygen (C.) and a map indicating the depth transect (D.), (modified from Expedition 323 Scientists, 2011).
Site U1344 is the deepest, coldest and highest in salinity of the seven sites drilled. It is currently located below the OMZ (which is strongest between ~650-1500mbsl), and has the highest dissolved oxygen concentration (~2mL/L) of the Expedition 323 Sites.

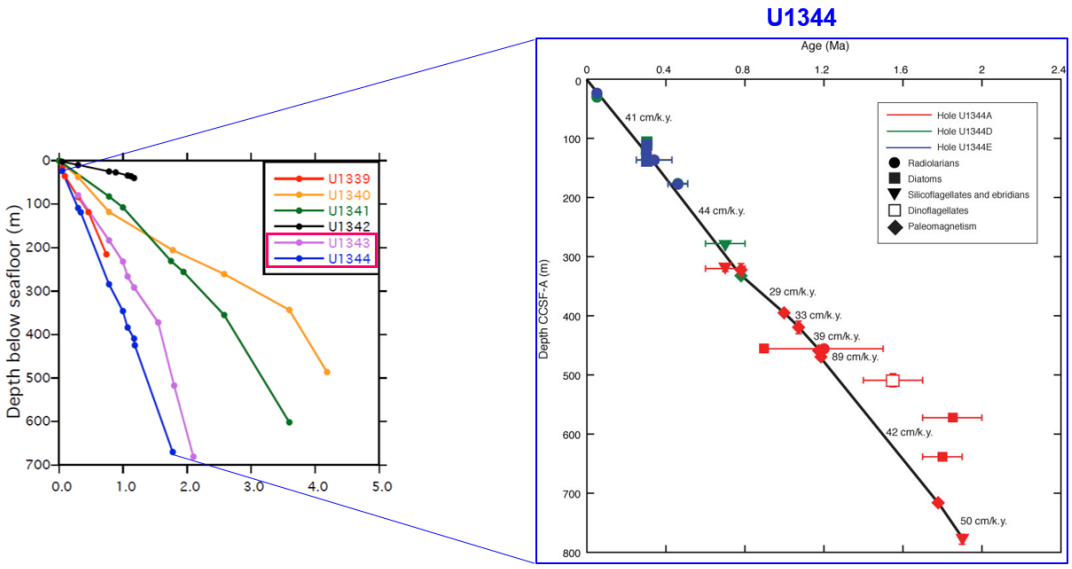

Figure 4: Expedition 323 Sites Sediment Age Model. Sedimentation rates versus time for Expedition 323 Sites. U1344 is indicated in blue, and U1343 is in purple. Both cores cover approximately the same time interval (modified from Expedition 323 Scientists, 2011).

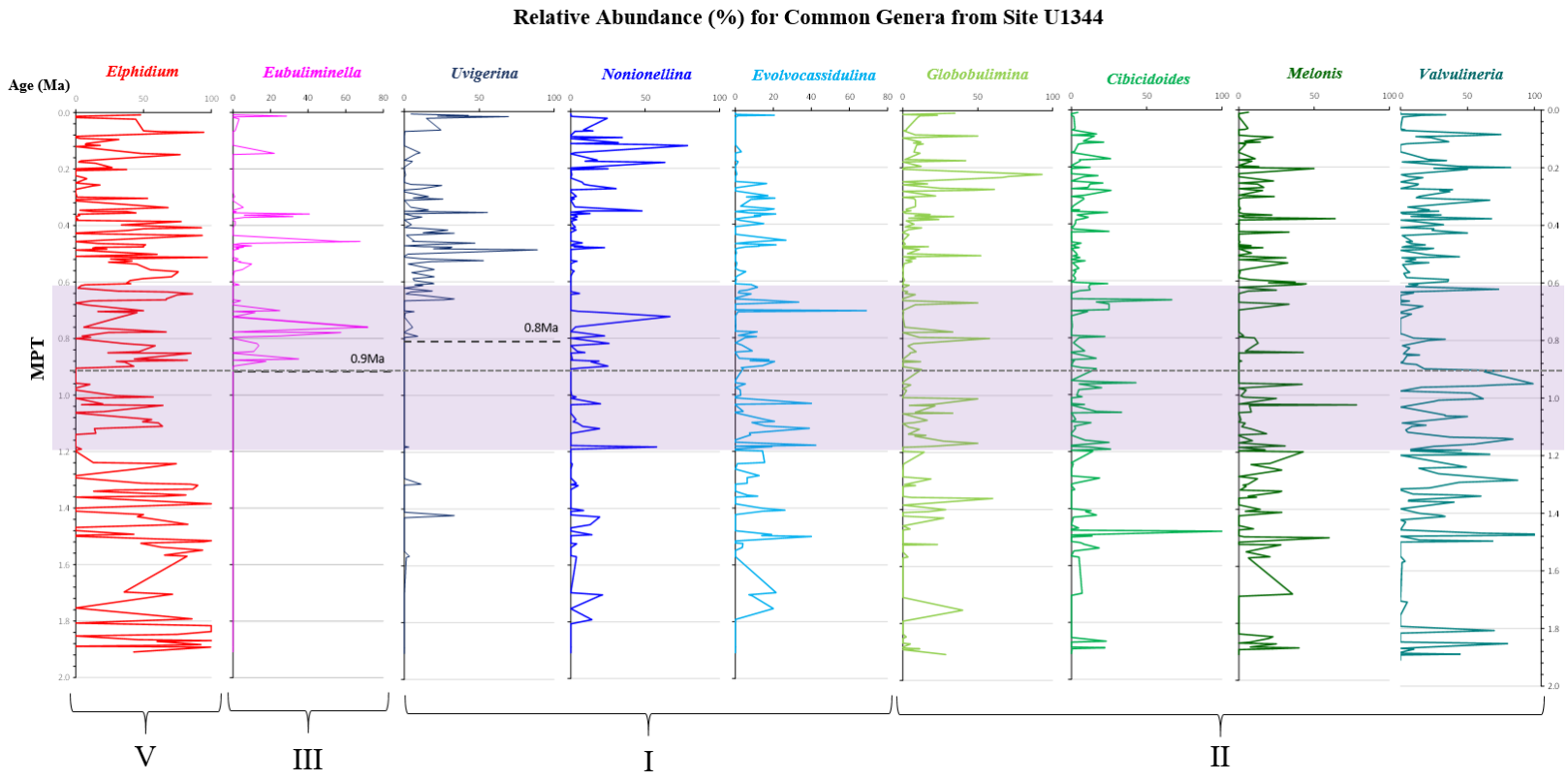

Figure 5: Downhole Relative Abundance of Benthic Foraminifera. Relative abundance (%) for 9 of the most common benthic foraminifera at Site U1344. Eleven total genera make up 1% or greater of the total population at Site U1344, the top 9 are shown above. The interval from 1.8-1.5 Ma shows very low abundance in all records, except *Elphidium*. Roman numerals indicate genera with similar down hole records

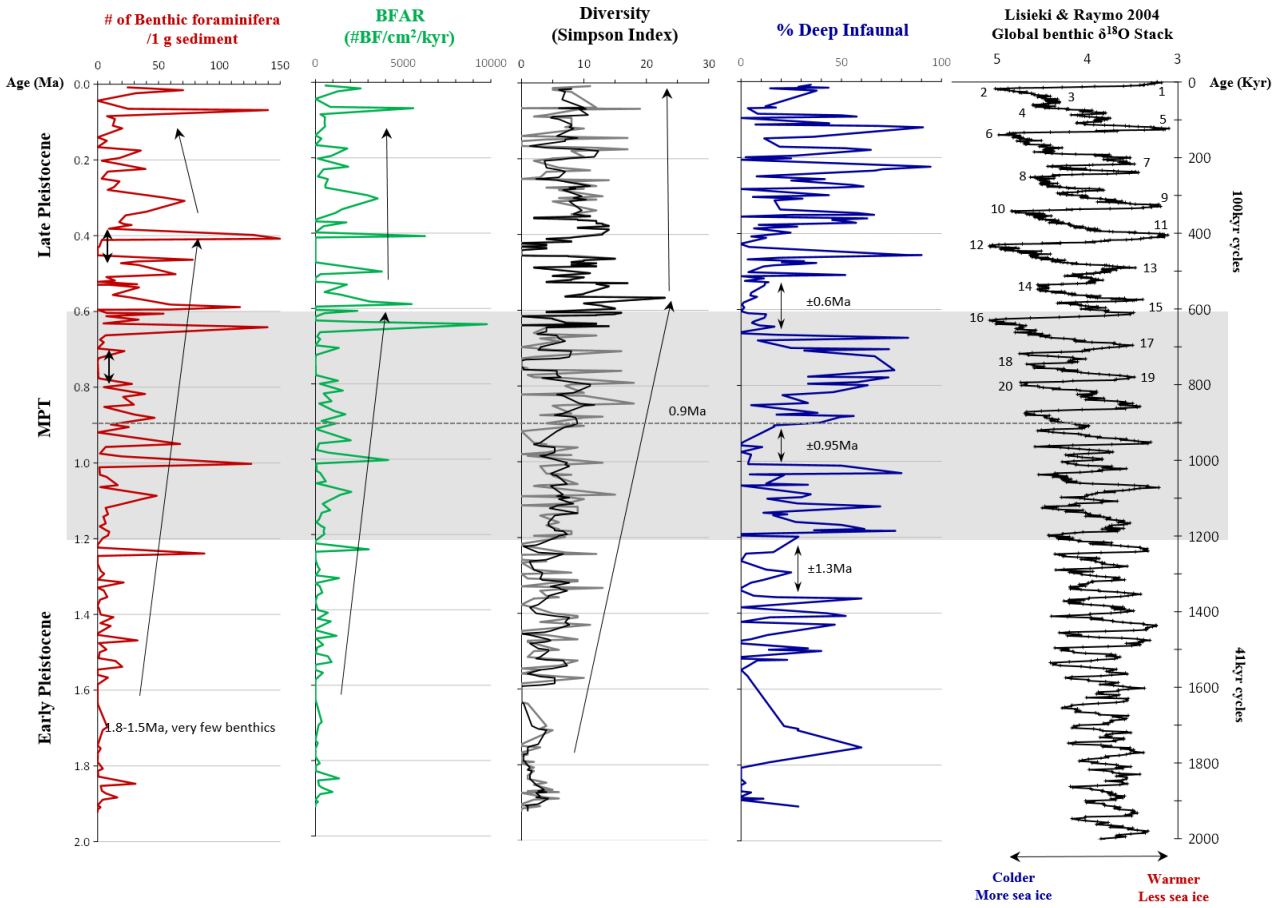

Figure 6: Downhole Trends in Abundance, Diversity, and BFAR. (From left to right), downhole records of benthic foraminifera counts (in #BF/1g),, Benthic Foraminifera Accumulation Rates (BFAR), Diversity (by the Simpson Index) with a moving average (black line), Relative Abundance of Deep Infaunal (%) and the LR04 climate record with the last 20 marine isotope stages in the "100kyr world" labeled

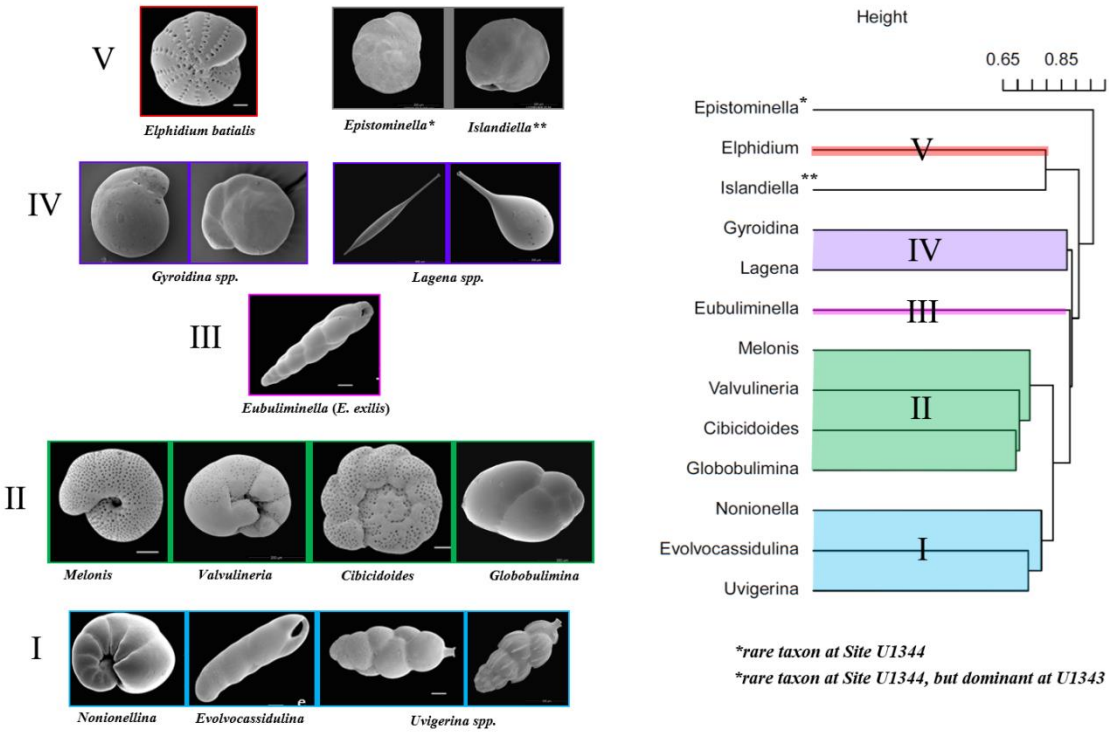

Figure 7: SEM Images and Statistical Cluster Dendrogram. Sixteen SEM images for the most common genera at both Sites U1343 and U1344. Multiple species are displayed for Gyroidina and Lagena, which are the rarest at both Sites. Right: For the 13 most common genera of benthic foraminifera at both Sites U1343 and U1344, the R-mode Cluster dendrogram is displayed using average linkage clustering. Horizontal scale (Height), on dendrogram measures degree of dissimilarity – in this case, by means of Bray-Curtis dissimilarity metric.

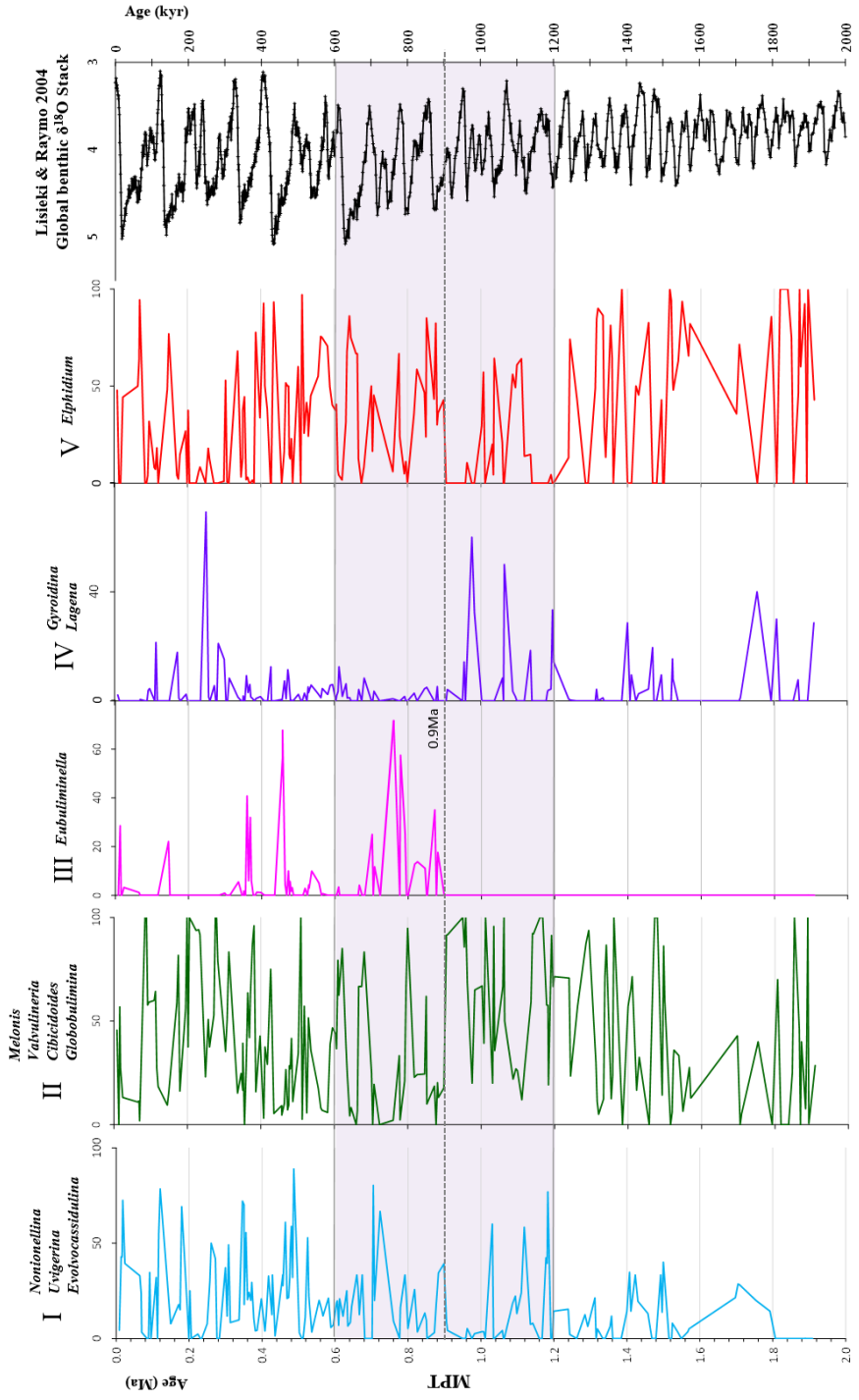

Figure 8: Benthic Foraminifera Assemblage Relative Abundance. Plots of Benthic foraminifera assemblages from Site U1344 are based on the cluster dendrogram (Figure 7). These plots highlight similarity in the records between Assemblages II and IV and Assemblages I, III, and V. and more clearly show trends in assemblages across the MPT.

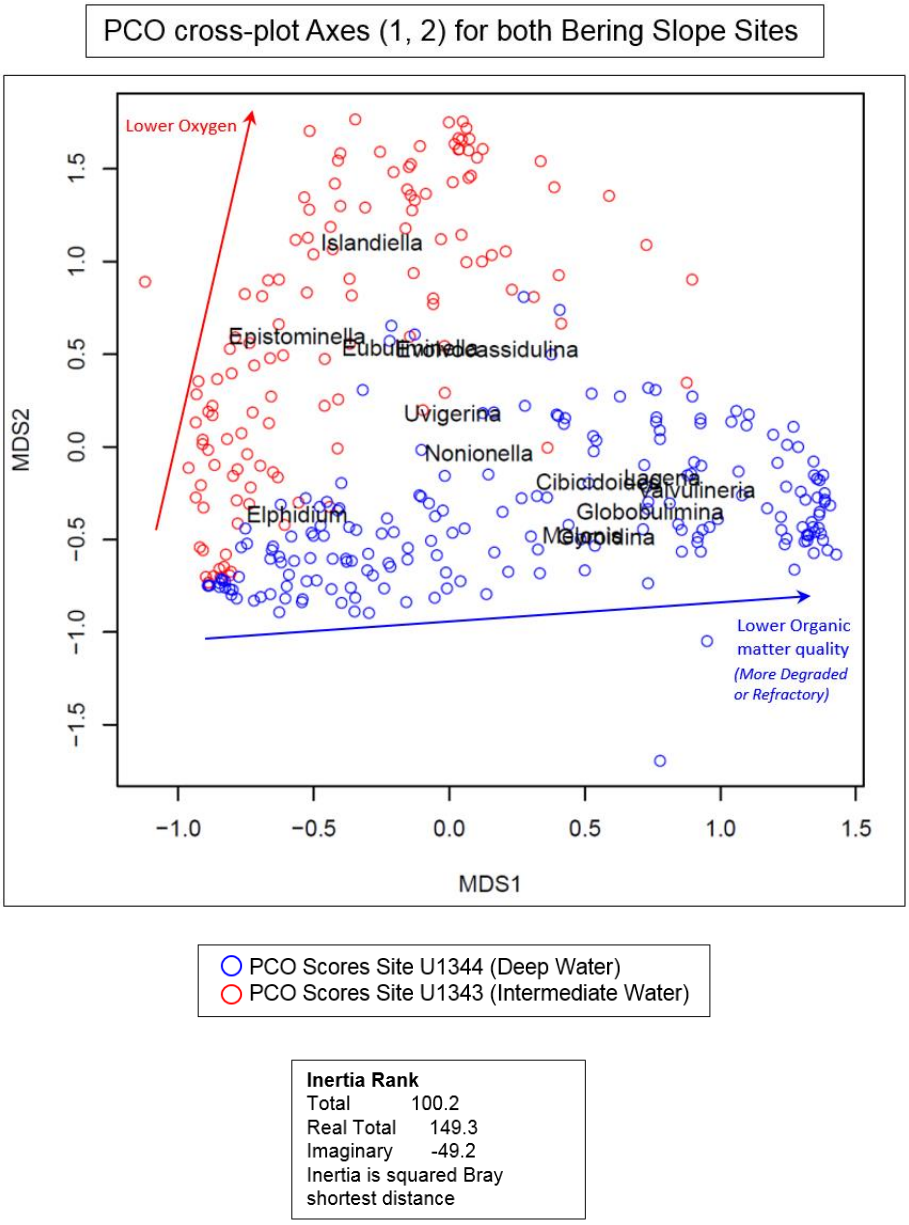

Figure 9: Principal Coordinate Analysis (PCO) of Sites U1344 and U1343. Site scores are plotted in red for U1343 and in blue for Site U1344. Genera names are overlain in black text. Distribution of PCO scores for U1344 are largely controlled by axis 1, whereas PCO scores for U1343 are primarily controlled by axis 2. Arrows indicate possible environmental parameters controlling distribution of species at each of the sites.

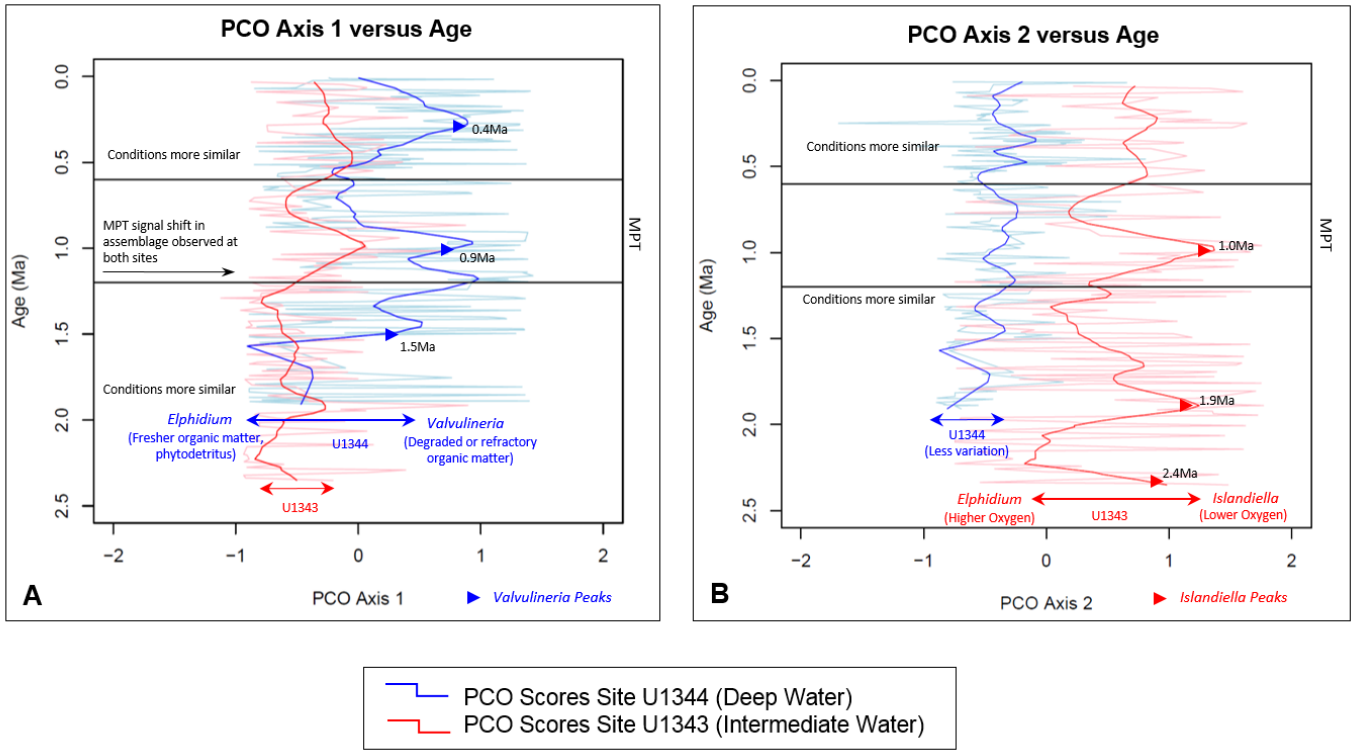

Figure 10: Principal Coordinate Analysis (PCO) versus Age. Plots for Bering Slope Sites U1344 and U1343 are distinguished by color. Panel A: PCO Axis 1 versus Age Panel B: PCO Axis 2 versus Age. Divergence from the *Elphidium*-end of the environmental gradient are indicated as peaks in either *Valvulineria* at Site U1344 (Panel A) or *Islandiella* at Site U1343 (Panel B).

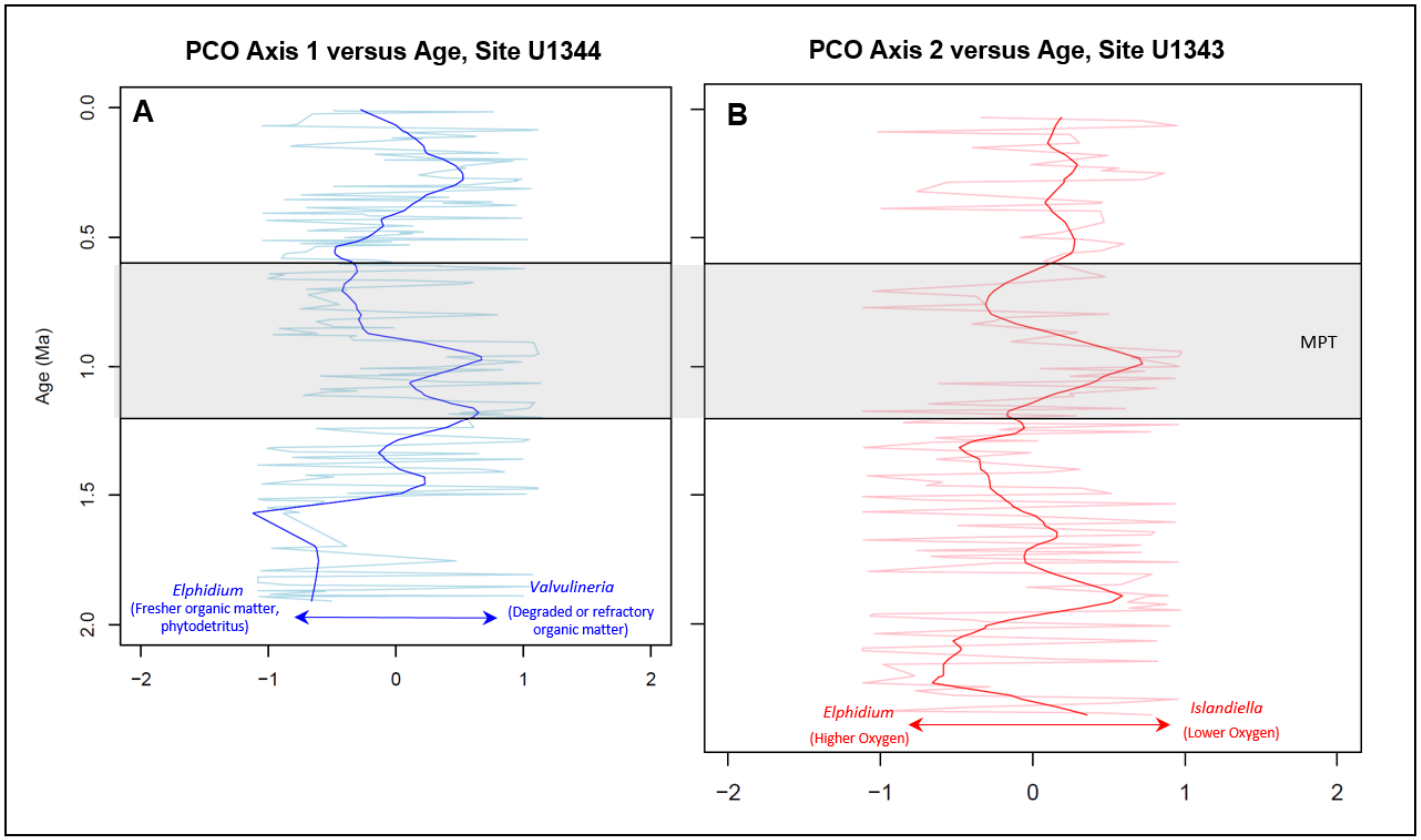

Figure 11: Individual Site PCOs versus Age. Principal Coordinate Analysis plots for Bering Slope Sites U1344 (Panel A: PCO Axis 1 versus Age) and U1343 (Panel B: PCO Axis 2 versus Age) are isolated in this Figure to allow for more clear trends in the primary environmental driver from each site. Note the vertical scale change as the fossil record for U1343 is longer (to 2.4Ma).